

Kaisa-Riikka Mustonen

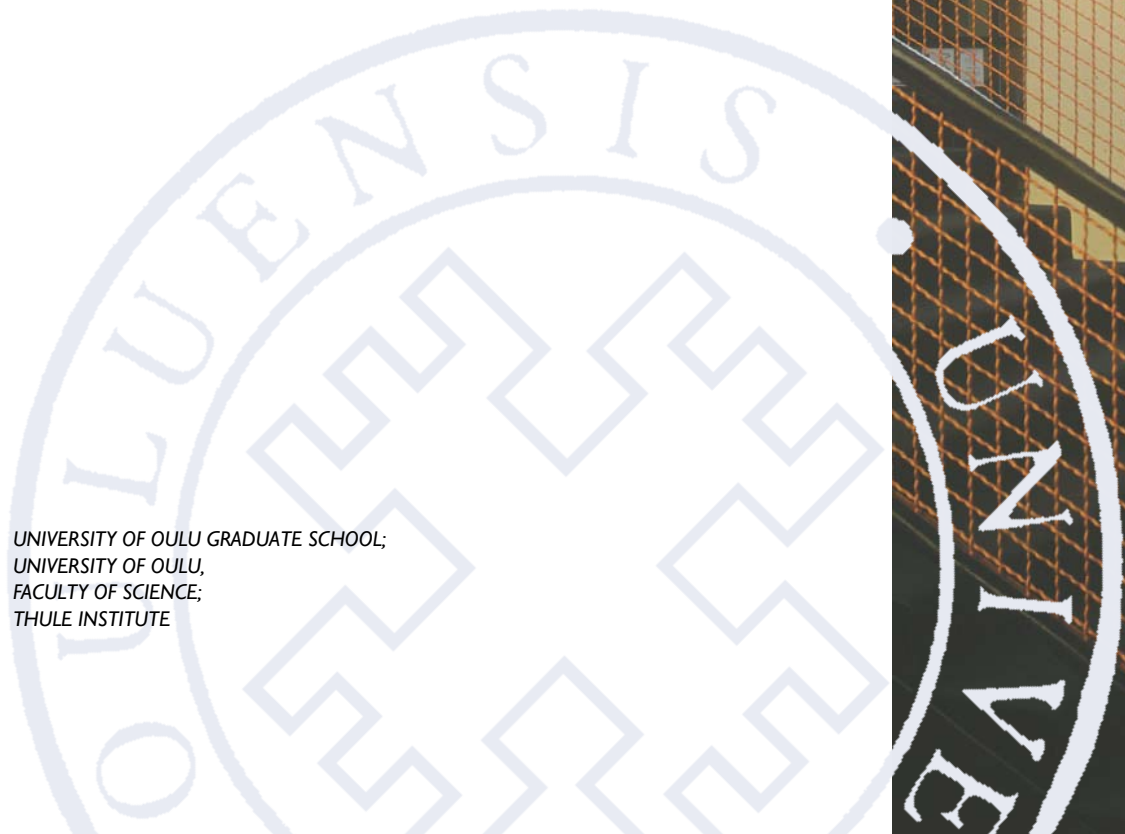
CLIMATE CHANGE AND BOREAL RIVERS

*PREDICTING PRESENT-DAY PATTERNS AND
FUTURE CHANGES IN HYDROLOGICAL REGIME
AND ITS EFFECTS ON RIVER COMMUNITIES*

UNIVERSITY OF OULU GRADUATE SCHOOL;
UNIVERSITY OF OULU,
FACULTY OF SCIENCE;
THULE INSTITUTE

A

SCIENTIAE RERUM
NATURALIUM



ACTA UNIVERSITATIS OULUENSIS
A Scientiae Rerum Naturalium 683

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**CLIMATE CHANGE AND BOREAL
RIVERS**

Predicting present-day patterns and future changes in hydrological regime and its effects on river communities

Academic dissertation to be presented with the assent of the Doctoral Training Committee of Technology and Natural Sciences of the University of Oulu for public defence in Kuusamonsali (YB210), Linnanmaa, on 25 November 2016, at 12 noon

UNIVERSITY OF OULU, OULU 2016

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Acta Univ. Oul. A 683, 2016

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ISBN 978-952-62-1417-7 (Paperback)
ISBN 978-952-62-1418-4 (PDF)

ISSN 0355-3191 (Printed)
ISSN 1796-220X (Online)

Cover Design
Raimo Ahonen

JUVENES PRINT
TAMPERE 2016

Mustonen, Kaisa-Riikka, Climate change and boreal rivers. Predicting present-day patterns and future changes in hydrological regime and its effects on river communities

University of Oulu Graduate School; University of Oulu, Faculty of Science; Thule Institute

Acta Univ. Oul. A 683, 2016

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Abstract

Although flow regime is a key element in determining the structure and function of lotic ecosystems, little is known about the variation of natural flow regimes and its relation to biological communities in highly seasonal northern boreal rivers. Temperature and precipitation patterns at northern latitudes are predicted to change drastically in the future causing severe effects on stream ecosystems. Interactions between climate change impacts and land use might further create unpredictable environmental stress. In this thesis, I first assessed the relationship of natural flow regimes of northern boreal rivers with taxonomic and functional structure of stream macroinvertebrates. Second, I combined hydrological, climate and biological models to study how climate change will alter northern flow and thermal regimes, how macroinvertebrates will respond to these changes and where these changes are going to be most pronounced. Third, I experimentally studied how different stream organisms are responding to flow change, sedimentation and their possible interaction. The role of hydrology in structuring macroinvertebrate assemblages was evident. Streams were predicted to lose much of the flow seasonality in the future, causing drastic changes that even exceeded the effect of future warming on macroinvertebrates. Especially communities within small seasonal streams were predicted to change, highlighting the importance of focusing conservation actions on these systems. Different organism groups exhibited highly variable responses to different stressors. For instance, aquatic fungi, which have been used less in climate change research, responded more strongly to flow change than traditionally used macroinvertebrates. The interactive effects of flow and sand were all antagonistic (i.e. less than the sum of the individual effects), which could be reassuring for management, although it means that both stressors may need to be removed to produce true ecological recovery. The results support the use of hydrological models in ecological studies for predicting current and future hydrological conditions at a site. However, as extreme events have been predicted to become more frequent, instead of modeling change in average conditions, future predictive models should be able to capture extreme fluctuations to gain more realistic view of climate change effects on stream ecosystems.

Keywords: aquatic fungi, benthic macroinvertebrates, biodiversity, boreal streams, climate change, ecohydrology, ecosystem functions, flow seasonality, flow variability, hydrological modeling, multiple stressors, sedimentation, stream community

Mustonen, Kaisa-Riikka, Ilmastonmuutos ja pohjoiset virtavedet. Virtaamaolosuhteiden yhteys jokiemme eliöyhteisöihin nyt ja tulevaisuudessa

Oulun yliopiston tutkijakoulu; Oulun yliopisto, Luonnontieteellinen tiedekunta; Thule-instituutti
Acta Univ. Oul. A 683, 2016

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Tiivistelmä

Joen virtaamaolosuhteet ja niiden vaihtelu ovat tärkeimpiä jokiekosysteemien rakenteeseen ja toimintaan vaikuttavia tekijöitä. Tästä huolimatta pohjoisen havumetsävyöhykkeen jokien luonnollisia virtaamaolosuhteita ja niiden yhteyttä virtavesieliöihin on tutkittu vähän. Ilmastonmuutoksen on ennustettu aiheuttavan voimakkaita muutoksia pohjoisten alueiden ilman lämpötilassa ja sadannassa, ja nämä muutokset tulevat mitä todennäköisimmin aiheuttamaan vakavia seurauksia myös jokiekosysteemeissä. Ilmastonmuutoksen ympäristövaikutukset voivat lisäksi aiheuttaa jo olemassa olevien ihmistoiminnasta aiheutuvien ympäristövaikutusten kanssa haitallisia ja vaikeasti ennustettavia yhdysvaikutuksia. Väitöskirjassani arvioin ensin pohjoisten virtavesien luonnollisten virtaamaolosuhteiden suhdetta pohjaeläinyhteisöjen taksonomiseen ja toiminnalliseen rakenteeseen. Tämän jälkeen tarkastelin yhdistämällä erilaisia ilmastonmuutoksen skenaarioita hydrologisen ja biologisen mallin kanssa, miten ilmastonmuutos saattaa tulevaisuudessa vaikuttaa jokien virtaamaolosuhteisiin ja niissä eläviin pohjaeläinyhteisöihin. Lisäksi arvioin missä ja minkälaisissa jokityypeissä ilmastonmuutoksen vaikutukset tulevat esiin kaikkein voimakkaimmin. Lopuksi tutkin kokeellisesti, miten virtaamavaihtelu ja hienojakoinen sedimentti ja näiden mahdolliset yhdysvaikutukset vaikuttavat eri virtavesieliöihin. Tulokset osoittivat, että vuodenajasta riippuvat virtaamavaihtelut vähenevät ilmastonmuutoksen myötä, minkä seurauksena pohjaeläinyhteisöissä tapahtuu voimakkaita muutoksia. Erityisesti pienten jokien pohjaeläinyhteisöjen monimuotoisuus ja koostumus muuttuivat verrattaessa tämän päivän lajistoa tulevaisuuden ennustettuun lajistoon. Eri virtavesieliöryhmät vastasivat hyvin eri tavalla virtaamavaihtelun ja hiekoittumisen aiheuttamaan elinympäristön muutokseen. Esimerkiksi akvaattiset sienet, joita on aikaisemmin harvoin käytetty ilmastonmuutostutkimuksissa, vastasivat voimakkaammin virtaamamuutoksiin kuin tutkimuksissa perinteisesti käytetyt pohjaeläimet. Kaikki kokeessa havaitut yhdysvaikutukset olivat kuitenkin pienempiä kuin yksittäisten vaikutusten summa. Tulos on huojentava vesiensuojelun kannalta, mutta tarkoittaa toisaalta myös sitä, ettei yksittäisten ihmisvaikutusten poistaminen välttämättä takaa vesistön ekologisen tilan parantamista, jos elinympäristöön vaikuttaa yhtaikaisesti useampi tekijä. Väitöskirjani tulokset tukevat hydrologisten mallien hyödyntämistä ekologisessa tutkimuksessa. Ilmastonmuutoksen myötä eri ääri-ilmiöiden, kuten rankkasateiden, on ennustettu tulevan entistä yleisimmiksi. Ääri-ilmiöiden vaikutukset ekologiin vasteisiin tunnetaan kuitenkin heikosti. Mallien kehittämisessä olisi tämän vuoksi jatkossa tärkeää keskittyä ääri-ilmiöihin ja niiden aiheuttamiin biologisiin muutoksiin, jotta voisimme nykyistä realistisemmin arvioida ilmastonmuutoksen vaikutuksia sisävesiekosysteemeissä.

Asiasanat: akvaattiset sienet, biodiversiteetti, boreaaliset virtavedet, ekohydrologia, ekosysteemin toiminta, hydrologinen mallinnus, ihmisvaikutukset, ilmastonmuutos, pohjaeläimet, virtaamaolosuhteet, virtavesieliöyhteisö vuodenaikavaihtelu

*We must begin thinking like a river if we are to leave a
legacy of beauty and life for future generations.
(David Brower)*

Acknowledgements

In a way, my journey through life has always been surrounded by rivers. My childhood home is located on the bank of river Oulujoki, and therefore many of my favorite things to do at home were more or less related to the river. Whether it was walking in the forest beside the river, going on a boat, swimming, fishing, exploring the hydropower station close by with my friends (although we were definitely not supposed to), ice skating, ice fishing, etc. – the list is endless. Also my favorite spot at my grandparents' farm was a small bridge going over river Poikajoki. I remember sitting there thousands of times and letting my mind wander while watching the endless flow of water. My father's father was a constructor worker at many of the hydropower stations built to tame the river Oulujoki back in the 50s. I remember seeing old photos of a huge free flowing river, and I remember my grandfather telling stories with a definite melancholy in his voice how the river used to have beautiful rapids full of fish that were there no more. I know that if my grandfather had had a choice, he would have preferred leaving our beautiful rivers run free. I believe all this has led me to this day where I now stand holding my own doctoral thesis which includes studies that give guidance in how to help our rivers to withstand the human-induced pressures of the future. Today, I hope, is just the beginning of my lifelong journey to protect our precious rivers. And I know that today I would make my grandfather proud.

If I told you the road leading to this day has been easy, I would be lying. Yet any hardness that has come with it is secondary, as the road has been full of amazing experiences, opportunities to learn new things, and possibilities to explore and study subjects that I feel passionate about. Most importantly, I wouldn't be here if there weren't these amazing people around me who have supported me throughout this journey. First of all I would like to express my gratitude to my principal supervisor Heikki Mykrä for your guidance and support throughout this process. I truly appreciate the way you trusted me to tackle the subjects independently from the beginning, and at the same time always had time for my problems and questions. I feel that during these five years, we have grown to be a pretty good team. I wish we can continue this collaboration in the future. Timo Muotka, you have been part of my university career from the very beginning. You supervised my bachelor's degree, then offered me work as a field assistant in your research group, which I did basically the whole time while finishing my master's degree, and then finally you guided me through the PhD as my second supervisor. I have learned a lot from you during these years, and

without your contribution to this thesis, it would not be as good as it is today. Bjørn Kløve, my third supervisor, thank you for all the support you gave me especially in the beginning of this process. We had a couple of discussions in the beginning about the role of hydrology in my thesis and you helped me to have confidence in myself that I am capable of handling that field also. Hannu Marttila, your help with all the hydrology related things has been priceless, and I have very much enjoyed working with you during these years. Noora Veijalainen and Kalle Sippel, thank you for all the help in understanding the processes included in the hydrological modeling. I also have to thank Mikko Tolkkinen and Annamari Markkola for helping me out with all the fungi, OTU, DNA and leaf litter related issues. Thank you goes also to my very good master's students Nico Alioravainen and Sirkku Mäkinen for all the lab work you did with the data from the experiment. Jari Oksanen – the statistical wizard in our department, thank you for helping me out with the trickiest statistical problems I faced. I also want to acknowledge the laboratory staff of the Biology department for all your help with the lab analyses. In addition, I would like to acknowledge the staffs of Kainuu Fisheries Research Station and Oulanka Research Station for all your help related to the experiment (paper III). I would also like to give special thanks to Chuck Hawkins who contributed a lot to the second paper of my thesis. Thank you and your whole family for making me feel at home during the three-month research visit in Utah. I'm also thankful for David Angeler and Núria Bonada for reviewing my thesis and giving constructive comments. I would also like to acknowledge Thule Institute for supporting my PhD project financially and also thank UniOGS, VALUE graduate school and Maa- ja Vesitekniikan tuki ry who have financially supported my studies, conference trips, research visits and finally finishing up my thesis.

Then I want to thank Pauliina Louhi for helping me to get involved in Stream Ecology Research Group by encouraging me 10 years ago to go to talk to Timo ("he won't bite") about my interest in stream ecology. Also, a special thanks to you for choosing me to do a master's thesis project with the best possible field team "Charlie and the Charlie's Angels". Kristian Meissner (Charlie), thank you for being a superb supervisor, and thank you for all the discussions we have shared. Thank you, of course, for all the horse magazines, posters and coloring pictures you've sent to cheer me up during my days with the PhD. And Saija Koljonen (the blond Angel), thank you for all the great laughs, the support during my studies, and making me remember that writing a thesis doesn't always have to be that serious.

One of the most important things during such a huge journey as writing a PhD is the peer support. I cannot emphasize enough how important you guys have been to me during this journey, and not just as co-workers but also as friends. Friends with whom to share the pressure and the anxiety when things are not going as planned, or share the joy when getting your first paper published or a grant proposal approved! And from this lot, a special thank you goes to my favorite namesake Kaisa Huttunen, for all the advices during my PhD, being great company at conference trips all around the world and the best possible lab partner to get dosed up with ETAX fumes. And also, thank you Romain, Maare, Kaisa L, Mira, Mari, Heli and everyone else who are or have been a part of the Stream Ecology Group. And of course, a big thanks to all my other fellow PhD students (most of them already PhDs) in the department, Nelli, Vekku, Tuomo, Netta, Mikko, Fantti, and of course all the rest from the most amazing group of friends called Käpyjengi, you know who you are. Thank you!

A special thank you must also go to my very dear friend Pinja. You have been the most awesome friend I could hope for. You have been part of the biggest and most meaningful events of my life so far, and I know you will also be there in the future. Thank you! And then my other girls: Tiina, Mari, Ansku and Saila a.k.a Vajakit/Marsuteam. You are simply the best! Without your friendship and support in the past few years, life would have been much more difficult and especially much more boring. In this group I also have to include Maija, although we haven't been as much in touch lately as we used to, thank you for the most awesome adventures during our master's studies. I love you all!

And then Partypilami – the band! Kata, Jersu, Ville, Juho, Jere. Thank you for all the super fun gig trips! Being part of this group and being able to sing in front of thousands of people with such an amazing and professional band in the background has been a dream come true for me. These shows all around Finland have been the best counterbalance I could hope for the PhD studies. Thank you, and let's keep rocking!

I also have to acknowledge my dearest four-legged friend Salli. No matter how hard the day has been, she has been there waiting for me and wagging her tail, and showing me what truly is important in life and how to enjoy and cherish the simplest things.

My interest towards biology is in no doubt due to my father. Thank you for taking me with you to the forest when I was a little girl and teaching me fascinating things about nature and its wonders. I thank you and mom for

supporting me on every step of my life. No matter what I wanted to do or become, you have never told me it would not be possible. Thank you, I love you.

And Ville, my one and only true love, the very best friend and the best companion for life I could ever hope for. Thank you for your endless support during this thesis project. Thank you for listening, thank you for being there, sharing the laughs and wiping the tears. Thank you for this amazing adventure so far, and thank you for standing beside me as we now are about to enter into the biggest adventure yet. I love you.

7.10.2016

Kaisa-Riikka Mustonen

Abbreviations

7Max	moving average of 7 days maximum flow
90Max	moving average of 90 days maximum flow
Abs Δ E	absolute change in expected taxonomic richness for a site
BC	Bray-Curtis dissimilarity between the reference and future macroinvertebrate assemblages
DFA	a stepwise discriminant function analysis
DH9	variability in annual maxima of 30-d means of daily discharge
DL5	mean annual minimum of 90-d moving average discharge
E	expected taxonomic richness for a site
Ec	current expected taxonomic richness for a site
Ef	future expected taxonomic richness for a site
Ef / Ec	proportion of expected current taxa predicted to occur in a future sample
FFG	functional feeding groups
FH6	flood frequency; the average number of events with discharges > 3x the median discharge
HIT	hydrologic index tool
IndVal	indicator species analysis
MA26	variability (CV) of monthly discharge values in March
MAAT	mean annual air temperature
MDF	mean daily flow
MH3	mean maximum discharge for March
MRPP	multiresponse permutation procedure
NMDS	nonmetric multidimensional scaling
OTU	operational taxonomic unit
PCA	principal component analysis
PCNM	principal coordinates of neighbor matrices
Pi	taxon-specific probability of occurrence
RA3	fall rate; change in discharge for days in which the change is negative
RAP	river analysis package
RDA	redundancy analysis
SSE	sum of squared error
TL2	variability in Julian date of annual minima
VEMALA	national-scale nutrient loading model for Finnish watersheds

WSFS Watershed Simulation and Forecasting System
 ΔE change in the expected taxonomic richness for a site

List of original articles

This thesis is based on the following publications, which are referred throughout the text by their Roman numerals:

- I Mustonen K-R, Mykrä H, Marttila H, Torabi Haghighi A, Kløve B, Aroviita J, Veijalainen N, Sippel K & Muotka T (2016) Defining the natural flow regimes of boreal rivers: relationship with benthic macroinvertebrate communities. *Freshwater Science* 35(2): 559–572.
- II Mustonen K-R, Mykrä H, Marttila H, Sarremejane R, Veijalainen N, Sippel K, Muotka T & Hawkins C (2016) Reduced flow seasonality as a key determinant of boreal stream invertebrate communities under climate change. Manuscript.
- III Mustonen K-R, Mykrä H, Louhi P, Markkola A, Tolkkinen M, Huusko A, Alioravainen N, Lehtinen S & Muotka T (2016) Sediments and flow have mainly independent effects on multitrophic stream communities and ecosystem functions. *Ecological Applications* 26(7): 2116–2129.

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1 Introduction

The physical environment of rivers and streams is defined by the movement of water, which determines the hydrological conditions of a river; i.e. the natural flow regime (Poff *et al.* 1997). The primary flow components of the natural flow regime are magnitude, frequency, duration, predictability and rate of change, and these factors are among the key elements determining the structure and function of lotic ecosystems (Poff *et al.* 1997). Hydrological variation, such as floods and droughts, can have direct effects on stream ecosystems by, for example, modifying habitats or directly affecting the amount of water, whereas indirect effects can arise from interactions with water quality or alteration of food resources (Lake 2000, Lytle & Poff 2004, Durance & Ormerod 2007). A number of studies have examined the influence of human-induced flow alterations on the structural (Poff & Zimmermann 2010) and functional (Statzner & Bêche 2010) responses of biological communities. However, to predict the consequences of human-induced land use or future climate change on flow regimes and stream ecosystems, we first need to understand the role of natural flow regimes in shaping the regional and local patterns of stream assemblages (Lytle & Poff 2004, Chinnayakanahalli *et al.* 2011).

Natural flow regimes of northern European streams and rivers are highly seasonal and strongly dominated by snowmelt, making their hydrological conditions highly variable yet relatively predictable (Korhonen & Kuusisto 2010, Veijalainen *et al.* 2010). Seasonality of boreal streams is driven by steady base-flow conditions during winter, high flood peaks during the spring snowmelt, variable summer flows and a secondary peak during autumn. Thus far, only few studies have examined the importance of hydrological factors in structuring stream assemblages in Nordic rivers (Friberg *et al.* 2013), and even these studies have been based on only a few hydrological measures or have focused on human-induced flow alteration. Therefore, little is known about the relationship between variation of natural flow regimes and biological communities in these snowmelt-dominated systems.

Stream and river ecosystems are highly vulnerable to the on-going climate change (Poff *et al.* 2012), and it has been reported that global-change induced decline in freshwater biodiversity may exceed that predicted for terrestrial and marine ecosystems (Xenopoulos *et al.* 2005, Strayer & Dungeon 2010). In addition, climate change has been predicted to impact river flow characteristics by the 2050s more than dam construction and water withdrawal (Döll & Zhang

2010). Northern boreal regions are predicted to experience the most drastic changes in temperature and precipitation regimes (IPCC 2013). In these regions, even small differences in temperature can change frozen ground status, precipitation phase (rain or snow), and the magnitude and timing of snow accumulation and melt (Arnell *et al.* 1999, Carey *et al.* 2010), which in turn can have dramatic effects on the highly seasonal flow regimes (Bring *et al.* 2016). Changing flow seasonality patterns can have severe effects on boreal stream communities (Wrona *et al.* 2016) by, for example, affecting the timing of emergence, reproduction, or growth and development of macroinvertebrates (Bêche *et al.* 2006, Power *et al.* 2008) and other aquatic organisms (Nilsson *et al.* 2013, Jardine *et al.* 2015). In addition to changing hydrological regimes, the future stream ecosystems are also influenced by increasing water temperatures. A number of studies have shown that warming air temperatures within the last few decades have already caused a detectable increase in surface water temperatures (Webb & Nobilis 2007, Durance & Ormerod 2009). Indeed, stream and air temperatures are often highly correlated (Durance & Ormerod 2009, Clews *et al.* 2010), and globally averaged air temperature increase of 2°C is estimated to lead to increases of annual mean river temperatures of ~1.3°C (van Vliet *et al.* 2011). Increasing water temperature can affect metabolism, physiology and bioenergetics of stream organisms (Durance & Ormerod 2007, Perkins *et al.* 2010, Woodward *et al.* 2010), eventually leading to changes in the structure (e.g. an increase of warm-adapted and decrease of cold-adapted species; Wrona *et al.* 2006, Domisch *et al.* 2013, Hill *et al.* 2014) and food web dynamics of stream communities (e.g. Perkins *et al.* 2010, Woodward *et al.* 2010).

Studies assessing the relationship between stream biota and the natural flow regime (or its change) are rare because the networks of gauging sites rarely have matching biological data. In addition, in near-pristine areas, headwater streams that are considered to contribute disproportionately to the biodiversity of river systems (Finn *et al.* 2011) are poorly represented in such networks (Hawkins *et al.* 2010, Poff *et al.* 2010b). However, catchment-scale hydrological models, developed for the prediction of hydrological conditions in ungauged streams, can provide a tool for predicting flow regimes across variable environmental settings (Poff *et al.* 2010b). Despite the apparent applicability of hydrological modeling, surprisingly few attempts have been made to apply this approach in ecological research (Kennen *et al.* 2008, Jähnig *et al.* 2012). A combination of catchment-scale hydrological models and climate change scenarios could be used to provide characterizations of future hydrological and thermal regimes of streams and rivers

(e.g. Chinnayakanahalli *et al.* 2011, Jähnig *et al.* 2012, Domisch *et al.* 2013) and, further, to predict the compositional change of stream communities.

Climate-change induced changes in temperature and precipitation patterns will affect ecosystems simultaneously with increasing anthropogenic land use. Climate change and catchment land use can introduce multiple and potentially interacting stressors to aquatic ecosystems by influencing both flow regimes and sedimentation processes (e.g. Wood & Armitage 1997, Bunn & Arthington 2002). In boreal regions, forestry is a major form of land use. Forest harvesting and draining of peatlands to increase forest growth can cause, for example, increasing erosion of sediments. Together with climate change induced hydrological change sediment erosion can cause interactive effects on stream ecosystems. Multiple, simultaneously operating stressors often yield non-additive responses (i.e., synergisms or antagonisms) that may be more common in nature than simple additive effects where the combined effect equals the sum of the effects of individual stressors (Darling & Côté 2008, Piggott *et al.* 2015b). For example, during low flow periods, fine sediments accumulate on the stream bed, potentially causing stronger negative effects (synergism) on stream organisms than predicted based on the additive effects of low flow and sedimentation (Dewson *et al.* 2007, Matthaei *et al.* 2010). Also, increased sedimentation during (or immediately after) floods may cause abrasion and therefore have a stronger negative effect on stream organisms than expected based on the additive effects of sedimentation and high flow (Bond & Downes 2003, Francoeur & Biggs 2006). Conversely, the combined effect of increased flow and sedimentation can also be less than the sum of the individual effects (antagonism) if, for example, floods remove accumulated sediments, thus revealing new areas for stream organisms to colonize (Mürle *et al.* 2003).

Multi-stressor impacts are among the greatest threats to global biodiversity (Sala *et al.* 2000), yet the full extension of these potentially harmful interactions remain largely unknown (Piggott *et al.* 2015a). While the number of multiple-stressor studies has been increasing, relatively few studies provide quantitative evidence of multiple-stressor effects in freshwater ecosystems (reviewed by Nöges *et al.* 2016). Furthermore, most previous studies have focused on a single organism group, usually macroinvertebrates (e.g. Bond & Downes 2003, Buendia *et al.* 2014). However, to more fully understand the effects of human stressors on stream ecosystems, it is important to include several taxonomic groups at different trophic levels and, in addition to traditional structural measures, measures of ecosystem function should also be included (Gessner & Chauvet

2002). The autumnal input of riparian leaf litter is the primary source of energy and carbon in many woodland streams, and microbes and shredding invertebrates are the key players in leaf decomposition. Thus far, however, multiple-stressor experiments have paid surprisingly little attention to leaf breakdown and especially microbial communities (but see Ferreira & Chauvet 2011, Wagenhoff *et al.* 2013).

Assessment of stressor impacts is complicated by the fact that many of these stressors are beneficial, or even necessary, at natural levels, but become harmful when exceeding the normal range ('subsidy-stress' effect; Odum *et al.* 1979). Despite the fundamental role of natural flow regime (Poff *et al.* 1997), flow alteration can act as a strong stressor in lotic ecosystems (Bunn & Arthington 2002, Döll & Zhang 2010, Poff & Zimmerman 2010, Wrona *et al.* 2016). Also sedimentation is a natural fluvial process, but when exceeding a certain level, it can turn into a stressor with severe effects on benthic macroinvertebrates (Jones *et al.* 2012), leaf decomposition (Sponseller & Benfield 2001, Niyogi *et al.* 2003) and periphyton production (Izagirre *et al.* 2009).

2 Aims of the thesis

The main objective of this thesis was to combine ecological and hydrological knowledge to produce information about natural flow regimes of boreal streams and rivers, to assess how and where the flow regimes and benthic communities of these rivers are likely to respond to climate change, and how climate change induced stressors are going to affect different stream organisms. Each subproject provides guidance for regional managers for the protection of rivers in the future as well as for the restoration of rivers already degraded by anthropogenic activities.

More specifically, I first (paper I) examined the characteristics of the highly seasonal northern rivers by first classifying 240 Finnish streams and rivers into different hydrological types, and then assessing how strongly the structure of macroinvertebrate assemblages corresponds to these stream types. The role of flow regime in shaping stream macroinvertebrate assemblages was studied by examining the relative importance of hydrological variables, local habitat, and geographical location to macroinvertebrate assemblages. In addition, I examined the relationship between hydrological variables and functional trait structure of benthic assemblages. Second (paper II), I predicted how these flow regimes will track future changes in thermal regimes, and how those changes are likely to affect taxon richness and community composition of macroinvertebrates, and where those effects are likely to be most pronounced. Finally (paper III), to reveal possible interactive effects of land use and climate change on stream ecosystems, I experimentally assessed the individual and interactive effects of flow change and sediment on benthic macroinvertebrate and leaf-decomposing fungal communities, as well as on two key ecosystem processes, leaf decomposition and algal biomass accrual.

2.1 Expected results

I expected the hydrological regimes to be strongly dominated by seasonality and snowmelt induced spring floods (paper I). In addition, I expected that taxonomic and especially functional structure of macroinvertebrate assemblages should be strongly related to hydrological conditions (Poff *et al.* 2010a, Stutzner & Bêche 2010), as flow regime is a key factor determining the structure and function of lotic ecosystems (Poff *et al.* 1997) and hydrological conditions, and other climate

dependent patterns can act as strong environmental filters selecting for specific traits in stream organisms (Poff *et al.* 2010a).

I further expected that any predicted changes in the most important hydrological factors characterizing boreal streams and rivers would be reflected as changes in macroinvertebrate assemblages (paper II). The strong latitudinal gradient in air temperature in northern Europe is paralleled by changes in the structure of freshwater assemblages (Sandin & Johnson 2000, Heino *et al.* 2003), suggesting that macroinvertebrate species distributions are strongly temperature-controlled. Therefore, I expected to see the most pronounced changes in macroinvertebrate assemblages in northern Finnish streams where the prospective temperature change is also greatest. In addition, as headwaters track air temperature (Caissie 2006) and precipitation (Gomi *et al.* 2002) more closely than do larger rivers, I expected macroinvertebrate communities to exhibit the most profound changes in headwater streams.

Finally, I expected strong interactive effects between flow variability and sand addition on stream communities and ecosystem processes (paper III). I expected sand addition to simplify stream habitats, and hence to have mostly negative effects on stream organisms (fungi, macroinvertebrates and algae).

3 Materials and methods

3.1 Study area and site selection

Finland is located in the coastal zone of the Eurasian continent between latitudes 60°N and 70°N and belongs to the temperate coniferous-mixed forest zone (Köppen 1936), with mean annual air temperature varying from -2 to 5°C and precipitation from 700 to 450 mm along a north-south gradient. Finnish climate shows both maritime and continental characteristics, as the Eurasian continental climate can occasionally extend to Finland, decreasing winter and increasing summer temperatures. At the boundary between the maritime and continental climate regimes, even a modest rise in temperature can alter substantially the spatial distribution and amount of snow cover, which in turn affects the timing of flow events, resulting in considerable changes in seasonal runoff patterns (Barnett 2005).

Papers I and II in this thesis are based on datasets provided by the Finnish Environment Institute and the University of Oulu. The study sites were selected from these datasets, with two restrictions. First, all sites had to be in pristine or near-pristine condition, thus only sites with no or only minor land use (<10% of the catchment cultivated; <5% urbanized) were included. Second, Finland was divided in three latitudinal zones: 60–63°N, 63–66°N and 66–70°N and, for each zone, we selected sites from four catchment size categories (<10 km², 10–100 km², 100–1000 km², >1000 km²) to ensure a geographically even distribution of different sized streams and rivers. Finally, we ended up with 240 stream sites across Finland sampled for benthic macroinvertebrates (Fig. 1).

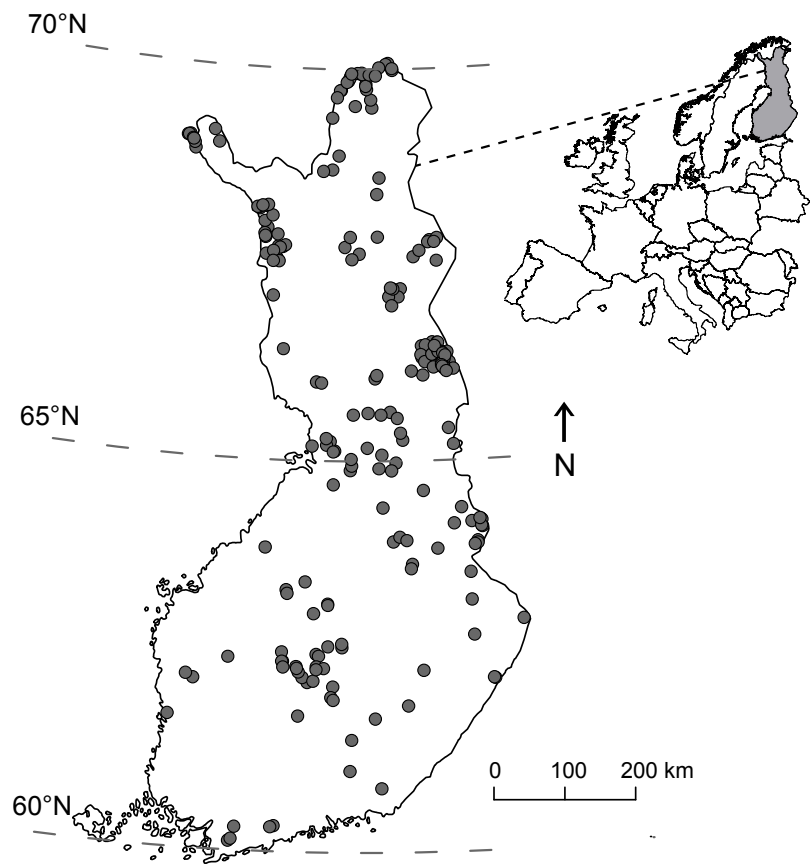


Fig. 1. Location of the study sites in Finland.

3.2 Hydrological data

We used the VEMALA model (Huttunen *et al.* 2016) based on a watershed simulation and forecasting system (WSFS) (Vehviläinen 2000), to calculate site specific daily discharges from the beginning of 1981 till the end of 2010 for all our 240 study sites (paper I and II). The VEMALA model is based on the same equations as the WSFS (Huttunen *et al.* 2016) and differs mainly in subcatchment division and calibration practices. It also includes smaller lakes, hence being more suitable for calculating discharges for small catchments (1st- and 2nd-order streams). VEMALA incorporates models for precipitation, snow accumulation and melt, soil, surface and ground water, and lake and river routing schemes. The models use daily precipitation and air temperature as input data and are constantly calibrated against an extensive national gauging network that includes measurements for snow-water equivalent, daily discharge, and lake water levels. Overall 223 flow indices, based on the modeled daily discharges, were calculated for each site by using the hydrologic index tool (HIT; Cade 2006) and the time series analysis module of the river analysis package (RAP; Marsh *et al.* 2003). All indices were calculated from raw daily series because standardization by long-term mean discharge equalizes the extremes and reduces variability of the flow data, which may influence hydrological classification (Chinnayakanahalli *et al.* 2011).

In paper II, the initial 30 year period (1981–2010) was used as a reference. Based on the modeled reference discharges, we calculated 72 flow indices for each site using the RAP tool. The 72 indices were selected based on results from paper I. In paper II, Colwell's flow predictability index (Colwell 1974) was divided into its two components; constancy (measure of temporal invariance) and contingency (measure of periodicity, i.e. seasonality). The constancy component is maximized when the flow is constant throughout the year, and the contingency (hereafter seasonality) component is maximized if the pattern of high or low flow occurrence is repeated across years.

3.3 Experimental setup

To experimentally assess the individual and interactive effects of flow change and sediment on stream organisms, an experiment was conducted at Kainuu Fisheries Research Station, Natural Resources Institute Finland (paper III). The experiment was established in six parallel artificial channels. All channels had a 20 to 30 cm

thick gravel/cobble bed and the amount of inflow was controlled individually via valves for each channel. Each channel was divided in two longitudinal sections to obtain twelve 0.75 m wide and 12 m long experimental flumes. After construction, flow level was equalized to intermediate level (30 cm/s) in all channels which then remained undisturbed for 70 days, allowing ample time for colonization by benthic organisms. In the beginning of the experiment, three different flow levels, low (~10 cm/s), intermediate (~30 cm/s) and high (~60 cm/s) were allocated to each of two randomly selected channels (Paper III, Fig. 1). Next, fine sediment (sand, grain size < 2 mm) was distributed evenly across one randomly selected flume in each of the six original channels, so that sand addition generated ca. 80% cover. The flumes with unmodified flow (intermediate) and no added sand served as control in statistical analyses. The experimental design thus consisted of two treatments: flow (three levels: low, intermediate, high) and sand addition (two levels: sand vs. no sand), with two replicate flumes for each treatment combination (Paper III, Fig. 1). After the treatments were established, the experiment ran for 17 days.

3.4 Biological data

Macroinvertebrate samples used in papers I and II consisted of four replicate 30-s kick samples (0.5 mm-mesh net) taken from swiftly flowing riffles from each of the 240 study sites. Each stream was sampled in autumn, mainly September, between 1998 and 2010. Macroinvertebrates were identified to species or genus, with the exception of a few dipteran and caddisfly families. In cases of taxonomic inconsistency, identifications were harmonized to a higher taxonomic level. Chironomids were not identified beyond family level and were therefore omitted from all statistical analyses. We also removed rare species (present at ≤ 3 sites).

Biological trait information for paper I was compiled using a freshwater ecology database (Schmidt-Kloiber & Hering 2015), information from few other European studies on benthic macroinvertebrates (e.g. Stutzner *et al.* 1994) and our own observations. To create the trait data set we used a fuzzy-coding approach (Chevenet *et al.* 1994) where all taxa are assigned with specific affinity values for each trait category. The trait information was compiled from different sources, so we standardized the affinities to sum to 10 for each trait.

Benthic macroinvertebrates in paper III were sampled from the experimental flumes by using a surber sampler (30 × 30 cm) with 0.5 mm mesh size. Sampling was conducted twice: a day before the onset of the experiment and at the end of

the 17-d experimental period. Four samples were taken in each flume each time. Samples were preserved in 70% ethanol and transferred to the laboratory where they were sorted and macroinvertebrates were identified to the lowest practical taxonomic level, usually species. In addition, macroinvertebrates were also collected from leaf bags used for measuring the effect of flow and sand on leaf breakdown.

In paper III, we filled 15 × 15 cm mesh bags with six grams of dried alder (*Alnus incana*) leaves. We used bags of two different mesh sizes: coarse mesh-size (8.0 mm) allowed invertebrates to enter the leaf bags whereas fine-mesh (0.2 mm) bags excluded invertebrates. In the beginning of the experiment, four bags of both mesh sizes were placed into each experimental flume. At the end of the experiment, leaf bags were collected and the remaining leaf litter was gently rinsed to separate it from other material. Leaf material was dried at 60°C for 24 h, then ashed at 550°C for four hours to convert dry mass to ash-free dry mass. Leaf breakdown was measured as a percentage leaf mass loss. A subsample was taken from each fine-mesh bag for the measurement of ergosterol content (used for the estimation of fungal biomass) and for the extraction of fungal DNA (used for studying fungal community structure). Ergosterol was extracted from freeze dried, pulverized leaf samples using modified ergosterol assay (Nylund & Wallander 1992). Ergosterol extracts were quantified with high-pressure liquid chromatography (HPLC) using a reverse-phase C18 column equipped with a precartridge and methanol as the eluent (1.0 mL min⁻¹, column temperature 30°C). Commercial ergosterol (5,7,22-Ergostatrien-3β-ol, Fluka AG) was used as standard. Results are expressed as ergosterol concentration in the litter (μg g⁻¹ litter DW). Fungal DNA was extracted from 0.07 g of leaf material using PowerSoil DNA Isolation Kit (MOBIO Laboratories, Carlsbad, CA co). rDNA coding regions were amplified using the fungal ITS primers 5'-CTTGGTCATTTAGAGGAAGTAA-'3 and 5'-TCCTCCGCTTATTGATATGC-'3. The amplicons were sequenced with Ion Torrent™ Personal Genome Machine® (PGM) System with 400-base read length chemistry method. All sequences were analyzed using the Quantitative Insights Into Microbial Ecology (QIIME) pipeline (Caporaso *et al.* 2010). The sequence library was split by samples and quality-filtered based on quality scores for each sequence. Sequences with quality scores below 25 were removed. Sequences shorter than 100 bp or longer than 1000 bp, as well as sequences with more than two mismatches in the primer, ambiguity, or maximum homopolymer run exceeding six were also removed. Sequences were clustered as OTUs (Operational Taxonomic Unit) using the

Usearch algorithm (Edgar 2010) with 97% sequence similarities. Because sequence numbers varied across samples, OTU datasets were rarefied to the lowest shared sample size (2076). Possible chimeras and OTUs that occurred in < 3 samples were removed from further analyses. Identification of chimeras and taxonomical assignment of OTUs was performed using BLAST search algorithm against the UNITE (Abarenkov *et al.* 2010) reference database. Since most fungal decomposers in aquatic systems are known to be Ascomycetes (Bärlocher 1992, Clivot *et al.* 2014), and Ascomycota was the dominant group also in our study, comprising 84.5% of all recorded OTUs, we excluded more sporadically occurring OTUs of other phyla from further analysis.

3.5 Environmental data

For paper I, we selected the most consistently measured environmental variables that characterized the local and catchment conditions of each site. Local-habitat variables were measured simultaneously with benthic sampling. In paper II we used only catchment scale environmental variables.

In the experiment (paper III) four transects perpendicular to flow were established at 3-m intervals in each experimental unit, and water depth (cm) and current velocity (cm/s, at $0.6 \times$ depth, MiniWater®20, Schiltknecht, Switzerland) were measured at regular intervals along each transect, with four measurements per transect. Sand cover was evaluated visually as percent cover in two 50×50 cm quadrates per transect. Depth, velocity and sand cover were measured in both the beginning and end of the experiment. In addition, water temperature and nutrient concentrations (total phosphorus and nitrogen) were measured at the inlet of the experimental system.

3.6 Predictive modeling

In paper II we used a combination of climatic, hydrological and biological models to predict future compositional changes to boreal stream macroinvertebrate communities. Five different climate scenarios, each incorporating a different combination of one global and one regional model, were used to predict future air temperatures and amount of precipitation (Paper II, table 1). Future daily discharges were simulated from 2070 to 2099 using the delta-change method (e.g. Arnell, 1996), where the observed regional air temperature and precipitation are varied according to each climate scenario. For each scenario, change in

temperature and precipitation was calculated by comparing the future monthly mean values for each grid cell (25×25 km) to corresponding values of the reference period (1981–2010). Since the increase in predicted mean annual air temperature (MAAT) and mean annual precipitation in Finland were virtually identical to predictions of the medium scenario (RCP4.5) in the latest (fifth) Assessment Report of IPCC (2013), we decided to only report results for scenario 4. The predicted temperature and precipitation values were used as input for the hydrological model VEMALA to produce predictions for future daily discharges (Fig. 2a). Based on the modeled future discharges, we calculated the same 72 flow indices for each study site as we had calculated before for the reference period.

RIVPACS-type (River Invertebrate Prediction and Classification System) multi-taxon niche model (Moss *et al.* 1987, Wright *et al.* 2000, Clarke *et al.* 2003) with random forest (Breiman 2001) was used to predict taxon-specific probabilities of occurrence (P_i) at each study site in the reference period. P_i values can be further summed to estimate the expected taxonomic richness for a site (E). We first included air temperature as the single default predictor in the model, and then used a forward selection procedure to include hydrological indices and catchment scale variables until improvement in model precision was negligible (Clarke *et al.* 2003, Van Sickle *et al.* 2005). Importance of individual predictors was evaluated by examining the variable importance plots with mean decrease in accuracy. The more the accuracy of the random forest decreases due to the exclusion of a variable, the more important the variable is (Breiman 2001). To examine the effect of climate change on macroinvertebrate communities, the final model was first run using variables from the reference period, and then rerun using the predicted future hydrological variables and air temperatures as predictors (Fig. 2b).

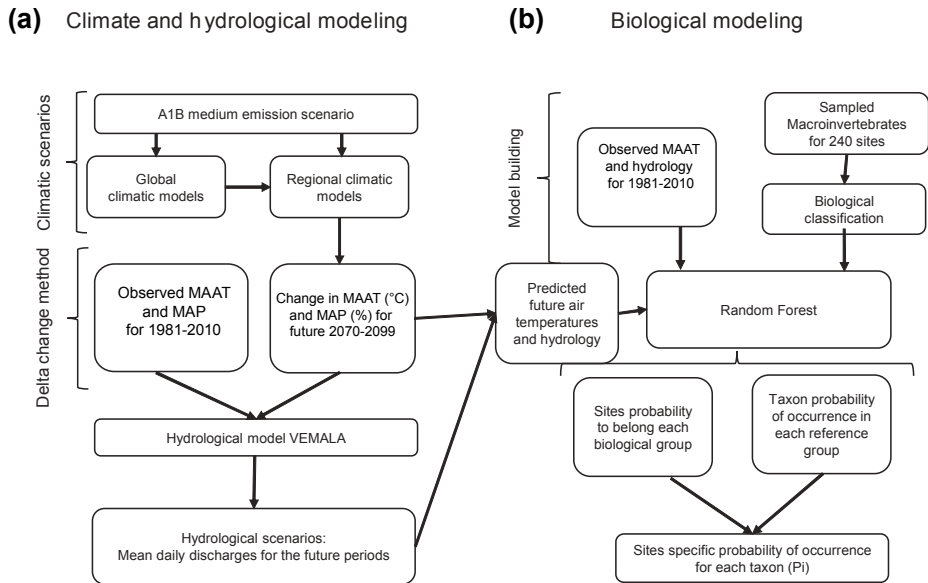


Fig. 2. Schematic presentation of the climatic-hydrological (a) and biological (b) modeling procedures. MAAT=mean annual air temperature, MAP=Mean annual precipitation.

3.7 Statistical analyses

All analyses were performed in R (R Core Team 2014), except stepwise discriminant function analysis (DFA; paper I) and the two-way ANOVA (paper II) which were performed with SPSS software (version 20.0, SPSS, Chicago, Illinois).

3.7.1 Analyses in paper I

Classification of 240 study sites into different hydrological regime types was based on methods by Olden *et al.* (2012). First, we used PCA on log-transformed hydrological variables to extract uncorrelated key hydrological gradients. Then, we selected the PCA components representing the most important hydrological dimensions based on the broken-stick method (Jackson 1993), whereby the components with eigenvalues exceeding the expected eigenvalues generated from a random data set are considered significant. To find the optimal number of

hydrological types, we clustered sites based on the PCA component scores and Ward's minimum variance method. The final number of clusters was based on the number of sites (>5) per group and the sum of squared error (SSE). As the number of clusters increases, SSE decreases. The appropriate number of clusters has been identified when the decrease in SSE between two sequential levels of clustering is substantial compared with the decrease between the subsequent levels (Everitt & Hothorn 2009). We used K-means clustering of PCA scores to classify our sites into the same number of groups as defined by Ward's method. Further, we used DFA analysis with Wilk's lambda to identify the hydrological indices that best discriminated between hydrological types.

The variation in the taxonomic structure of macroinvertebrate assemblages among different hydrological types was examined using NMDS and MRPP analyses with Bray–Curtis dissimilarity and Hellinger-transformed macroinvertebrate abundance data (R package *vegan*, Oksanen *et al.* 2013). MRPP is a nonparametric method designed to test differences in assemblage structure among groups defined a priori (Zimmerman *et al.* 1985). When the test statistic *A* reaches its maximum value of 1, communities within the defined groups are identical. When *A* approaches 0, the within-group heterogeneity becomes equal to that expected by chance, and when $A < 0$, heterogeneity exceeds that expected by chance. We tested significance of the null hypothesis of no differences among hydrological types by means of Monte Carlo procedure with 1000 permutations. We also used IndVal analysis (Dufrene & Legendre 1997) with R package *labdsv* (Roberts 2012) to identify potential indicator taxa for each hydrological type. IndVal analysis determines an indicator value (IV) for a species in each a priori defined site group (hydrological type). We considered species with $IV > 25$ (and significant at $\alpha = 0.05$) as meaningful indicators (Dufrene and Legendre 1997).

RDA analysis (Legendre & Legendre 1998) was used to examine the relationship of the taxonomic structure of macroinvertebrate assemblages to local-habitat and hydrological variables. To maintain the link with hydrological classification, we used the 18 most important hydrological variables separating the hydrological types according to previous DFA analysis. In addition, we included two hydrological variables with the highest loadings on each of the nine most important PCA components of hydrological variables to allow a more comprehensive presentation of flow regimes. Forward selection prior to RDA was conducted based on Hellinger-transformed species abundances and a two-step procedure for variable selection (Blanchet *et al.* 2008). Next, we used partial

RDA to partition the variation in taxonomic structure among hydrological variables, local-habitat variables, and spatial structuring (see Legendre & Legendre 1998). For the description of the spatial structure, we computed PCNM (Borcard & Legendre 2002) that generates multiple spatial variables that model spatial structures at different scales. The first eigenvectors with larger eigenvalues model large scales, whereas those with smaller eigenvalues model at progressively smaller scales. PCNM, forward selection, and RDA were done with R package *vegan*.

The relationship between biological traits and the selected hydrological variables were examined using the three-table ordination technique RLQ (Dolédec *et al.* 1996) and fourth-corner analysis (Legendre *et al.* 1997, Dray & Legendre 2008) with R package *ade4* (Dray & Dufour 2007). RLQ was used first to summarize the multivariate associations between hydrology and biological traits. RLQ combines the three separate analyses of tables R (hydrological variables \times sites), L (species \times sites), and Q (traits \times species) and aims to find the main relationships between environmental gradients and traits mediated by species abundances (Dolédec *et al.* 1996). The significance of the relationships was tested with a Monte Carlo procedure with 9999 permutations. We further used fourth-corner analysis to examine the significance of bivariate associations between single traits and hydrological variables. Fourth-corner analysis links the tables R, Q, and L and measures this link by Pearson correlation coefficient (for details, see Legendre *et al.* 1997, Dray & Legendre 2008). The significance of correlations was tested by permutation procedure (9999 permutations) with a sequential test that controls the type I error rate, as suggested by ter Braak *et al.* (2012).

3.7.2 Analyses in paper II

To study the effects of climate change on macroinvertebrate taxonomic richness, we first calculated the current expected number of taxa at a site (E_c) by summing the P_i values for all taxa on each site derived from the biological model for the reference period (see section ‘predictive modeling’). To calculate the expected number of taxa at future sites (E_f), we summed the P_i values from the biological model that used the predicted future air temperatures and hydrological conditions as input. To calculate E_c and E_f for a site, we used P_i values ≥ 0.00001 (i.e. all observed taxa included). We also calculated the change in taxonomic richness for

each site (ΔE) by subtracting E_c from E_f values, and the absolute change in richness ($Abs\Delta E$) by taking the absolute value of ΔE .

To study changes in macroinvertebrate assemblage structure, we used taxon-specific P_i values to calculate Bray-Curtis dissimilarities (BC) between the reference and future macroinvertebrate assemblages. In addition, we calculated the E_f/E_c ratio, which represents the proportion of expected current taxa predicted to occur in a future sample. If there is no change in taxonomic composition between the reference and future conditions, the ratio should be close to 1. When calculating the E_f/E_c ratio, a taxon was included only if its current P_i value was ≥ 0.5 , or if it was predicted to have $P_i \geq 0.5$ in the future. This was done to assess whether the reference assemblages based on core taxa are likely to change in the future.

We further studied the effects of stream size (catchment area: small $<10 \text{ km}^2$, medium = $10\text{--}100 \text{ km}^2$, large $>100 \text{ km}^2$) and latitude (south = $60\text{--}63^\circ\text{N}$, middle = $63\text{--}66^\circ\text{N}$ and north = $66\text{--}70^\circ\text{N}$) and their interaction on $Abs\Delta E$, BC, and E_f/E_c using two-way ANOVA. Prior to analysis, $Abs\Delta E$ and E_f/E_c were log-transformed to decrease heteroscedasticity. In case of a significant interaction, we used simple effect tests with pairwise comparisons (Least Significant Difference) to compare the means of one factor at each level of the other factor (and vice versa).

To examine the responses of macroinvertebrate assemblages to individual predictors, we built a new random forest model, separately for each community measure, and included the initial values of all selected predictors and their change as predictors in the final model. The importance of individual predictors was evaluated as mean decrease in model accuracy (Breiman 2001). In addition, we used partial dependence plots to visualize the relationships between a response variable and a predictor, independent of the influences of other predictors (Friedman 2001).

3.7.3 Analyses in paper III

In paper III, we first used a simple linear model fitted with R function `lm` in R package `stats` to test whether the sand cover at the end of the experiment differed between flow levels. To analyze differences among treatments in algal biomass, leaf breakdown, fungal biomass and OTU richness, and macroinvertebrate abundance and richness, we used linear mixed effects models with function `lme` in the R package `nlme` (Pinheiro *et al.* 2014). Three flow levels (low,

intermediate, high), and two levels of sedimentation (sand, no sand) and their interaction were used as fixed factors. In model selection procedure (top-down strategy; Zuur *et al.* 2009), channel was initially included as a random factor, but was removed from the final models if supported by the log-likelihood ratio test and comparison of AIC values of the proceeding models. Benthic samples taken before the experiment were used as a covariate to control for any among-channel variation in macroinvertebrate abundances unrelated to our experimental design. The effects of sand addition and flow were further examined as standard main effects, i.e., by pooling across factor levels. We also examined differences in the abundances of functional feeding groups (FFG; Merritt & Cummins 1996) and the most abundant macroinvertebrate species. For leaf-shredding macroinvertebrates, we used the leaf-bag samples, as these can be assumed to be more representative of organisms directly involved in leaf decomposition than are the benthic samples. Leaf breakdown in coarse-mesh bags was corrected for decomposition in fine bags (breakdown coarse minus breakdown fine) to obtain the fraction of decomposition attributable to detritivore feeding and physical abrasion (McKie *et al.* 2006). All variables were log-transformed before analysis, as with log-transformed data, the interaction term tests the multiplicative model of multiple-stressor effects (for more details see Sih *et al.* 1998).

NMDS analysis was used to visually examine the variation in fungal and macroinvertebrate community structure among treatments. PERMANOVA analysis was used to further test if differences in community structure between treatments were statistically significant. PERMANOVA partitions variation in a distance matrix according to any linear model, includes multifactorial designs, and returns P-values from a permutation procedure with pseudo-F ratios (Anderson & ter Braak 2003). Both analyses were performed with R package vegan (Oksanen *et al.* 2013) using Bray-Curtis distances of log-transformed community data. In addition, we used IndVal analysis to identify potential indicator taxa for each treatment, and also tested the association of leaf breakdown with fungal biomass (ergosterol content), total shredder abundance, and abundances of the two most abundant shredder taxa using Pearson correlations.

4 Results and discussion

4.1 Flow regimes of boreal streams and their relation to macroinvertebrate assemblages

We identified six distinct hydrological stream types (paper I, table 2). As expected, all types were strongly shaped by seasonality and snowmelt-dominated spring floods (paper I, Fig. 2). Seasonal flow patterns and a few size-related variables were the main factors discriminating among the types (paper I, table 2). The hydrological types partly followed the strong north-south climatic gradient of Finland (paper I, Fig. 1), as the northern and southernmost streams were quite strictly divided into two separate groups. The southernmost sites were characterized by high interannual variation in late autumn and winter discharges, reflecting the variable precipitation and higher temperatures of southern Finland (paper I, table 2, Fig. 2). The northernmost sites had stable flows during the winter because of stable snow cover and variable floods during spring and summer because of strong snowmelt domination followed by a long recession until the beginning of the next snow accumulation (paper I, Fig. 2). The remaining four hydrological types were distributed across the country, and mainly separated by factors related to flow variability, predictability or magnitude. This suggests that adjacent streams within the same climatic or geographical region cannot be grouped automatically into the same hydrological flow type, and detailed characterization of the flow regime of individual streams is needed (Chinnayakanahalli *et al.* 2011). In addition to the large-scale climatic gradient, hydrological stream types were strongly related to measures of flow magnitude. Flow magnitude is directly related to catchment size, which controls the mean annual flow, further influencing the structure of lotic communities (e.g. Sabo *et al.* 2010). Two of our hydrological types included sites with larger catchments compared to other types (paper I, table 2), suggesting that the south-to-north gradient in flow characteristics was partly overridden by size-related factors. As variation in macroinvertebrate assemblage structure is associated with stream size (e.g. Malmqvist & Mäki 1994), we did not want to obscure this relationship by standardizing for catchment size and grouping different-sized streams together (Chinnayakanahalli *et al.* 2011).

MRPP analyses showed that macroinvertebrate assemblage structure differed significantly among the hydrological types ($p < 0.001$). Although most

hydrological types were well separated in the NMDS ordination space, we found wide variation within and overlap among some types (paper I, Fig 3a). This was also shown as relatively low A-statistic of MRPP analysis ($A = 0.074$). Nevertheless, the strength of the hydrological classification (A-statistic of MRPP) was about the same as has been reported for the a priori defined European Union Water Framework Directive (European Commission 2000) system A typology (Mykrä *et al.* 2009) or ecoregions (Heino *et al.* 2007), suggesting that our hydrological classification was equally effective in accounting for the variability of macroinvertebrate assemblage structure in Finnish streams. Furthermore, we did find significant indicator taxa for all hydrological types (paper I, table 3). These taxa mostly reflected regional or size-related factors separating the hydrological types. For example, the biggest streams were indicated by taxa that are typically found in larger rivers, and the hydrological type with the northernmost sites was characterized by taxa that occur mostly in the northern parts of Finland. Several hydrological types with significant indicator species included different-sized streams scattered throughout Finland (paper I, Fig. 1, table 2), however, suggesting that also other than regional or size-related hydrological factors were playing a role in structuring these communities.

Although the hydrological typology was not very efficient in explaining the variation of macroinvertebrate composition, hydrology as a continuous composite variable in RDA was clearly a better descriptor of assemblage structure than were local habitat or space (paper I, Fig. 3). The most important hydrological variables explaining variation in macroinvertebrate assemblages represented flow magnitude based on mean or spring time maximum flows (MH3, 90Max, MA26), or were otherwise related to flow seasonality (DH9, TL2). Hence, results of RDA analysis clearly indicated the fundamental importance of hydrological factors to stream macroinvertebrate assemblages. However, the minor importance of local habitat variables may be partly an artifact caused by the limited number of local-habitat variables available to us. For example, water temperature (Friberg *et al.* 2013) and water-chemistry variables (e.g. nutrient content; Heino *et al.* 2007) can influence macroinvertebrate assemblage structure in boreal rivers but were not included in our study. The strong legacy of the last glaciation could also partly explain the relatively weak importance of local-habitat variables (Johnson *et al.* 2004), as northern European freshwater ecosystems support a relatively restricted species pool and collection of traits that allow residence in these harsh environments (e.g. physiological tolerance, high dispersal capacity). Importance of hydrology was further confirmed when the association between hydrology and

trait structure was examined in more detail. Results of the RLQ analysis showed that functional traits were significantly related to hydrological variation in ($p = 0.001$, paper I, table 4) and further, 35 significant relationships between individual trait categories and hydrological variables were revealed in the fourth-corner analysis (paper I, Fig. 4). Organism size and microhabitat preference were the traits most frequently correlated with individual hydrological variables (paper I, Fig. 4). The significant relationship of these traits and flow characteristics was not surprising, since many life-history traits scale with body mass (Woodward *et al.* 2005) and microhabitat preference categories were related mostly to substrate size, which often varies with flow conditions (e.g. Poff *et al.* 1997). Although we found significant correlations between traits and flow magnitude, the hydrological variables that most often correlated with different trait categories were 90Max, FH6, DL5, and RA3, all of which describe variability or seasonality of flow (Paper I, Fig. 4). This result suggests that functional traits may respond more readily to alteration of hydrological regimes whereas taxonomic structure may be more related to stream size.

4.2 Changing hydrological and thermal regimes and their effects on macroinvertebrates

According to our biological model, macroinvertebrate species distributions during the reference period (1981–2010) were strongly temperature-controlled, as variability of current macroinvertebrate assemblage composition was best explained by MAAT (paper II, Fig. 1). The final model included seven predictors, with MAAT being the most important, followed by MDF, 7Max, lake area percentage, coniferous forest percentage, peat land percentage and flow predictability. Also the perception that high-latitude regions are expected to warm the most (IPCC, 2013) was supported by our results (paper II, Fig. 2). Changes in macroinvertebrate assemblage structure measured as Bray-Curtis dissimilarity paralleled the larger change in MAAT at northern latitudes, with the exception of a few northwestern sites (initially the coldest sites in our data) where the assemblage structure was predicted to change less compared to other northern sites (paper II, Fig. 3). Instead of temperature change, however, the most important predictor for the change in macroinvertebrate assemblages structure was initial (reference period) MAAT (paper II, Fig. 5). Partial dependence plots showed that assemblages in sites initially warmer than $+2^{\circ}\text{C}$ had the lowest BC values (paper II, Fig. 5). These southernmost sites may already harbor taxa that

tolerate warm temperatures, and therefore these communities should not change as much as those in currently colder streams. Although the compositional changes between current and future assemblages were minor at these sites, the predicted change in the expected number of taxa (ΔE) mainly decreased (paper II, Fig. 3), most likely because there was no predicted immigration from more southerly regions, i.e. those outside the model range. This result is not necessarily a model artifact, however, because the dispersal of aquatic invertebrates across the Gulf of Finland may be very slow.

Dissimilarity in assemblage structure between current and future sites was highest at sites with initial MAAT around 0°C , and also relatively high for sites with initial MAAT lower than -3°C (paper II, Fig. 5). In contrast, ΔE exhibited least change at sites with initial MAAT around 0°C and initially coldest sites changed the most, and mostly positively (paper II, Fig. 3, Fig. 5). This result suggests that cold-adapted species are shifting northwards and being replaced by more tolerant southern species (Daufresne *et al.* 2007, Durance & Ormerod 2007), and hence the taxa number remains relatively constant in Middle Finland, although the compositional structure is changing. Furthermore, at the coldest northwestern sites, the mean air temperature was predicted to remain close to zero, causing relatively minor changes in the snow-melt dominated hydrological regime. For example, maximum flows were predicted to decrease throughout the country, yet remain relatively constant at these particular sites (paper II, Fig. 2). Warming of the initially coldest sites was thus not predicted to affect the distributions of cold adapted species, suggesting that these sites could serve as thermal refugia in the future.

The results of paper I showed that these high latitude river systems have highly predictable seasonal flows, and hydrological variables related to flow seasonality were among the most important factors explaining the taxonomic and functional structure of macroinvertebrate communities. Indeed, change in flow predictability was the second most important predictor, even more important than temperature change, for explaining the future changes in macroinvertebrate assemblages (paper II, Fig. 5). Change in predictability was significantly correlated with change in its seasonality component (Pearson $r = 0.60$, $p < 0.001$) but not with change in its constancy component ($r = 0.12$, $p > 0.05$). Therefore, the change in predictability index mainly reflected changing flow seasonality. Further, sites with the greatest predicted BC values or taxa loss (negative ΔE) were located in northeastern Finland. These sites are currently showing the strongest flow seasonality and their seasonality was also expected to change the

most (paper II, Fig. 6). These sites also harbor the most species rich contemporary macroinvertebrate assemblages, due to their unique environment that represents the westernmost remnants of pristine taiga forests (Malmqvist *et al.* 2009). The bedrock of the area is variable, with extensive occurrences of calcareous rocks. The geological and topographical heterogeneity is reflected in exceptionally diverse macroinvertebrate communities, particularly of mayflies (see Malmqvist *et al.* 2009). The region is characterized by continental climate with cold winters and warm summers, hence having a strongly seasonal flow regime. These results suggest that the predicted shift in flow seasonality will modify the biodiversity of boreal streams, even more so than does the increased water temperature (see Durance & Ormerod 2009). In addition, due to their isolated nature, biota in these unique environments may be particularly vulnerable to climate change.

As expected, taxonomic richness in our study was predicted to change more in headwater and mid-order streams than in large rivers (paper II, Fig. 4). The bigger effect of climate change on smaller rivers was not surprising, since they track air temperature more closely (Caissie 2006) and are also more vulnerable to low flows and flash floods than are larger rivers that have a large storage capacity that can buffer against climatic variability (Stahl *et al.* 2010, Blöschl 2013). However, dissimilarities between current and future macroinvertebrate assemblages of large rivers in Middle and Northern Finland were as high as in other stream size classes (paper II, Fig. 4), suggesting that changes in temperature and hydrological regimes in the northernmost regions will alter macroinvertebrate assemblages also in large rivers.

4.3 Individual and interactive effects of flow change and sand on stream communities

Contrary to our expectations, the results from the experiment (paper III) showed that sand and flow had only few interactive effects on biological responses (paper III, table 2). Algal biomass measured as chl-a concentration clearly increased in high-flow conditions, particularly when sand was absent, but sand addition reduced this positive effect, resulting in a strong antagonistic interaction between the two stressors (paper III, Fig. 2). Matthaei *et al.* (2010) suggested that interactions between sediment and flow should be more pronounced for biota directly exposed to current (e.g. algae and macroinvertebrates on stone surfaces). Indeed, the other interactive effects found in our study were species-specific responses of two benthic macroinvertebrate taxa. Abundance of the caddisfly

Hydropsyche pellucidula declined significantly with sand addition but only in the intermediate flow (paper III, Fig. 6), whereas the crustacean *Asellus aquaticus* was less abundant in flumes without sand but only in high-flow conditions (paper III, Fig. 6), leading to significant interactions in both cases. The few interactive effects were all antagonistic by nature (paper III, table 2), supporting the perception that antagonistic effects may be more common in nature than are synergistic effects (Darling & Côté 2008, Jackson *et al.* 2016). The predominance of antagonistic effects has been reported to be characteristic of freshwater ecosystems, which therefore seem to be, on some level at least, able to minimize the net effects of multiple stressors (Jackson *et al.* 2016).

In general, species-specific responses by macroinvertebrates to both stressors were generally more prevalent than changes in aggregate community measures (i.e. abundances of functional feeding groups). Both stressors also had positive effects on some species. For example, abundances of the leaf-shredding caddis larva *Lepidostoma hirtum* (paper III, Fig. 5,6) responded positively to sand, which is usually considered harmful for stream organisms. These results indicate potential subsidy-stress effects, and highlight the importance of characterization of the responses of individual taxa and the use of aggregated variables only after having distinguished the magnitude, direction, and uncertainty in the responses of individual community members (King & Baker 2010). Furthermore, in addition to individual species, also organisms at different trophic levels exhibited highly variable responses to the same stressor. For example, sand addition had a positive effect on shredder abundances in both leaf bag (paper III, Fig. 5) and benthic (paper III, Fig. 6) samples, yet it clearly decreased algal (paper III, Fig. 2) and fungal biomass (paper III, Fig. 3). In addition, our results indicated that structure and function may be rather loosely related, as shredder-mediated breakdown in coarse-mesh bags only responded to flow (paper III, Fig. 2) despite the clear effect of sand on shredding macroinvertebrates. This emphasizes the need to monitor both communities and ecosystem process rates (McKie & Malmqvist 2009) when studying multiple-stressor effects on stream ecosystems.

We expected leaf mass loss to be highest in the high-flow treatment with added sand, as abrasion can enhance leaf breakdown (Lepori *et al.* 2005), but, surprisingly, leaf mass loss was highest in low-flow conditions, and there was no evidence of physical fragmentation in any of the treatments. It has been speculated that breakdown rate could increase as a result of stimulated microbial activity in microhabitats stabilized by low flow and sediments (Magbanua *et al.* 2013). In our experiment, however, sand addition systematically decreased the

microbe-mediated leaf breakdown in fine-mesh bags (paper III, Fig. 2), indicating harmful effects of sedimentation on microbial communities independent of flow level (see Cornut *et al.* 2010, Danger *et al.* 2012). One explanation for the decreased leaf breakdown rate in flumes with added sand could be induced bacterial breakdown in low flows, but we did not analyze bacterial biomass in our leaf bag samples. Nevertheless, NMDS analysis showed that fungal communities differed between flow levels (paper III, Fig. 4) and we also found a positive relationship between fungal biomass and leaf breakdown (paper III, Fig. 3), which both indicate the primary role of fungi in the decomposition of leaf litter in our experiment.

Higher leaf mass loss in low flows might also be related to compositional changes in fungal communities. According to the IndVal analysis, OTUs associated with purely aquatic species were strong indicators of high-flow conditions, whereas indicators of low flows were mostly endophytic terrestrial fungi (paper III, table 1). Low-flow conditions can reduce dispersal and attachment of aquatic hyphomycete spores (Schlieff & Muntz 2009), hence plant endophytic fungi already present in leaf litter might benefit from low flow to the extent that they might have been able to outcompete aquatic hyphomycetes (see Clivot *et al.* 2014). However, while DNA sequencing allows microbial species identities and abundances to be detected, it does not tell us which species contribute to decomposition and by how much. A more direct approach would involve assessment of RNA sequences, as they are involved in the transcription of nucleic acids to proteins and therefore indicate generalized metabolic activity. Baldrian *et al.* (2012) observed high RNA/DNA relationships in some microbial taxa in soils and concluded that much of the metabolic activity may be caused by relatively rare species. Therefore, also high activity by the few aquatic hyphomycetes indicative of low flow conditions (paper III, table 1) might explain the high leaf mass loss. Nevertheless, not even RNA sequencing indicates which ecological functions are being performed or which taxa contribute most to the breakdown process (Bärlocher 2016). More research on the functional roles of fungal taxa of different origin is clearly needed, but our results do suggest that terrestrial fungi may also contribute to leaf decomposition in the aquatic environment (see also Clivot *et al.* 2014).

5 Conclusions: future studies and implications for management

Despite the fundamental role of river flow in determining the structure and function of lotic ecosystems (e.g. Poff *et al.* 1997), few studies have directly related features of the natural flow regime to variation in stream invertebrate assemblage composition in northern European rivers. Therefore, the first goal of this thesis was to obtain a more comprehensive view of the natural flow regimes of these highly seasonal rivers. Although statistical estimation of streamflow characteristics has been the standard approach for estimating hydrologic conditions of rivers for decades, it has rarely been used in ecological flow studies (Knight *et al.* 2012, Murphy *et al.* 2013). Results of this thesis clearly indicate the potential of applying catchment-scale hydrological models for the prediction of hydrological conditions in ungauged streams. Furthermore, this approach clearly revealed the fundamental role of hydrology in determining the taxonomic and functional structure of stream macroinvertebrate assemblages in northern streams and rivers. Hence, hydrological models might also be applied to improve the performance of predictive bioassessment models by enabling the inclusion of year-to-year climatic variability (Huttunen *et al.* 2012).

By combining the used hydrological model with climate change scenarios and a predictive biological model, we were able to predict the consequences of the changing climate on macroinvertebrate communities via its effects on stream flow and water temperature. Although temperature was an important factor shaping future benthic communities, our results emphasize the influence of the future hydrological change. Macroinvertebrates can tolerate wide variation in temperature and their upper thermal limit increases with acclimation (Dallas & Rivers-Moore 2012). Hence, as temperature change will be relatively slow and local habitat factors (riparian shading, groundwater input) may mitigate the effects of warming, the predicted increase in water temperature might not be lethal to many stream organisms. Future studies should integrate laboratory experiments and field observations to improve our understanding of the fundamental and realized thermal niches of stream organisms (Hill *et al.* 2014, Woodward *et al.* 2016). The importance of the hydrological change was evident, and change in flow seasonality was predicted to have stronger effects on macroinvertebrate biodiversity than does temperature change. Flow seasonality is the most pervasive hydrological characteristic of northern rivers, thus it is not surprising that changes in flow seasonality also had profound effects on stream

communities. Results of paper I suggested that functional traits of macroinvertebrates could respond more readily to flow alteration and seasonality, whereas taxonomic structure is more related to stream size due to its closer relation to magnitude measures of flow. However, most of these magnitude measures described snowmelt induced spring time maximum flows, which are undoubtedly also strongly related to flow seasonality, further supporting the strong relationship between macroinvertebrate communities and flow seasonality in northern European rivers. Nevertheless, flow seasonality, and its change, are related to stream size, as the predicted future changes in flow predictability and maximum flows were more pronounced (albeit not significantly so) in small and mid-order streams than in larger streams, further leading to bigger predicted changes of macroinvertebrate assemblages in smaller rivers. Hence, small and strongly seasonal headwater streams already threatened by land use activities (Strayer & Dungeon 2010, Finn *et al.* 2011) should be given special attention in freshwater conservation activities, since they seem to be more vulnerable to climate change than larger rivers.

Change in seasonality of northern river systems is strongly correlated with temperature, as warming causes changes in the timing and amount of snowmelt which then affect seasonality patterns. Therefore, seasonality of flow includes both a hydrological and a thermal signal and would therefore be expected to be a stronger predictor of macroinvertebrate communities than is temperature alone. However, strong biodiversity effects of altered flow seasonality may not be limited to streams with snowmelt-dominated hydrographs. For example, in the tropics, temperature is quite constant throughout the year, and flow seasonality is due to annual changes in precipitation patterns. Tropical rivers with rhythmic annual floods have been reported to have higher fish species richness, more stable avian populations, and elevated rates of riparian forest production compared to systems with arrhythmic annual flood pulses (Jardine *et al.* 2015). As climate change has been predicted to alter seasonal flow regimes across the world (Döll & Zhang 2010, IPCC 2013), changes in flow seasonality may be critical for all stream ecosystems in seasonal environments.

Changes in thermal and hydrological regimes in the northernmost regions were predicted to alter macroinvertebrate assemblages also in larger rivers. Many larger northern European rivers are already altered by the construction of hydropower plants, impoundment of water and regulation of outflows, with dramatic consequences to their natural flow regimes and river ecosystems and their biota (Poff *et al.* 1997, Bunn & Arthington 2002, Poff & Zimmerman 2010).

Hydropower plants alter the natural seasonal flow patterns by reducing flow during high-flow periods and increasing flow during low-flow periods, causing environmental degradation of downstream ecosystems (e.g. Bunn & Arthington 2002). A massive amount of restoration projects has been initiated to reverse the negative impact of human induced flow alteration in the past few decades. For example, modified dam operations (reoperations) where hydropower dams release water in a pattern more closely resembling the natural flow regime have been suggested as a practice to improve the ecological status of altered flow regimes (Richter & Thomas 2007, Watts *et al.* 2011). As flow seasonality is a key factor structuring stream assemblages in northern rivers, reoperation practices that restore the seasonal flow patterns, planned in collaboration among water resources engineers and conservation ecologists, could mitigate, on some level at least, the ecological impacts of regulation on these rivers (Poff *et al.* 2016). Incorporating ecological knowledge into future dam operations might also assist with adaptation to the impacts of climate change on seasonal flow patterns (Watts *et al.* 2011, Poff *et al.* 2016). However, ecosystems of these tamed rivers are already degraded at such a high level that these actions would never truly restore ecosystem integrity. In addition, this could only be applied to larger rivers with dam constructions, and the most vulnerable headwater streams would still suffer the full impact of changing hydrological patterns.

Comprehensively addressing the importance of changing flow seasonality would require a more holistic view of the mechanistic effects of flow seasonality on different stream organism groups. The results of this thesis showed that organisms at different trophic levels may exhibit highly variable responses to the same stressor (flow change or sedimentation). Although macroinvertebrates are useful indicators of the biological condition of aquatic ecosystems (e.g. Wallace & Webster 1996, Bonada *et al.* 2006, Allan & Castillo 2007), assessing the impact of climate-change induced hydrological change also for other organism groups is essential. For example, fungal communities seemed to be highly responsive to flow change in our experiment, suggesting that they might be even more affected by changing flow patterns than are benthic macroinvertebrates. Results of the experiment further emphasized the need to monitor both stream communities and ecosystem process rates (McKie & Malmqvist 2009), as leaf breakdown rate and taxonomic measures responded differently to the studied stressors (see also Gessner & Chauvet 2002).

The stream organisms in our experiment responded more often to sand addition than to flow change, adding to the body of evidence that sedimentation is

a pervasive and often predominant human stressor in lotic ecosystems (e.g. Jones *et al.* 2012, Piggott *et al.* 2012). Biological responses to flow variability were generally much weaker than those caused by sand; for example, the positive effect of high flow on algal accrual was overridden by sand addition. This sort of asymmetry between two stressors in their single effect sizes has been suggested to explain the prevalence of antagonistic interactions in freshwater ecosystems (Jackson *et al.* 2016). From the management perspective, this observation highlights the importance of identifying antagonistically interacting stressors, because both stressors may then need to be removed or moderated to produce any substantial ecological recovery (Piggott *et al.* 2015b, Jackson *et al.* 2016). Species-specific responses to stressors were generally more prevalent than changes in aggregate community measures, implying that considering individual species is important for the detection of stream impairment (King & Baker 2010). Hence, studying the responses of individual macroinvertebrate species to changing hydrological regimes with similar approach as used in paper II might reveal additional information about the future of macroinvertebrate assemblages of northern boreal rivers. Furthermore, macroinvertebrate assemblage composition was predicted to respond more consistently than taxonomic richness to future changes in flow and thermal regimes, suggesting that species replacement instead of extinctions is the main mechanism altering macroinvertebrate assemblages. This observation may have important ecosystem-level implications, particularly if species with key functional roles are replaced by other species with different functions (Perkins *et al.* 2010, Wrona *et al.* 2013). Species most likely to replace others are probably the ones that better track the shifting climate due to their higher dispersal capacity (Pearson 2006). If these species replace more specialized species (which are often more sensitive to climate change; Poff *et al.* 2012), this could lead to increasing homogenization of communities (i.e. decreasing beta diversity) in the future (Socolar *et al.* 2016), with potentially strong management implications, as taxonomic homogenization may result in a loss of functional diversity and ecosystem services and, eventually, reduced community resilience under disturbances (e.g. Johnson & Angeler 2014).

Sites in papers I and II were in near-pristine condition, thus providing a baseline for the reference-condition approach in biomonitoring where the 'ecological status' of a site is based on its deviation from the reference (Wright 2000, Hawkins *et al.* 2000). Results of this thesis add to the line of evidence that this baseline is shifting from the earlier reference condition (Woodward 2010) and

hence currently used biomonitoring programs will need to be modified to accommodate climate-change induced alteration of stream biodiversity in northern rivers. Shifting reference conditions also need to be taken into account in future restoration projects, as current restoration goals might be unachievable in the future (e.g. Palmer *et al.* 2008). In addition, the interaction of climate change and land use can cause unpredictable degradation of already impacted sites. For example, high nutrients and runoff (as a result of urbanization) combined with increasing water temperature (as a result of climate change) can cause further declines in macroinvertebrates and fish diversity (Mantyka-Pringle *et al.* 2014). Re-establishing riparian woodlands can improve the conditions of degraded aquatic ecosystems by, for example, binding sediments and nutrients before they enter waterways. Furthermore, planting of riparian trees along headwaters can allow adaptation to climate change by reducing warming of stream water via increased shading, and potentially increase macroinvertebrate biomass and enhance resilience by increasing basal resources (Thomas *et al.* 2016). Hence, allocating restoration resources into re-establishing riparian zones might help the already degraded (e.g. by intensive forestry) boreal streams to mitigate the interactive effects of climate and land-use change.

Climate change is expected to affect sedimentation processes, most likely via increased input of fine sediments and greater (and less predictable) variability of stream flow. It is therefore reassuring that these two stressors did not have strong (if any) synergistic effects on the biological responses we examined. However, as boreal streams are expected to have more variable hydrographs in the future, with more frequent and extended periods of droughts and floods (IPCC 2013), the effects of flow-related stress may not have been well captured by our experiment. Clearly, forthcoming studies should manipulate these and other human stressors in experiments that run for much longer periods, focusing on the impacts of multiple simultaneously operating stressors on stream communities and ecosystem functions. Future experiments should also focus on longer-term effects where these stressors act as press rather than pulse (as in our study) disturbances. However, extreme events, such as episodes of strongly increased precipitation, temperature and flow, have been predicted to become more frequent (IPCC 2013), having profound consequences on northern stream ecosystems (Nilsson *et al.* 2015). Therefore, more information of the effects of strong pulse disturbances is also needed. In addition, similar to paper II, most research on the predicted effects of climate change in freshwaters has been based on modeled changes in average historical conditions. As extreme events are predicted to become more common, a

more holistic framework including predictive models capable of capturing the effects of forthcoming environmental fluctuations are needed for a more comprehensive understanding of the climate-change induced effects on stream ecosystems (see Woodward *et al.* 2016).

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- I Mustonen K-R, Mykrä H, Marttila H, Torabi Haghighi A, Kløve B, Aroviita J, Veijalainen N, Sippel K & Muotka T (2016) Defining the natural flow regimes of boreal rivers: relationship with benthic macroinvertebrate communities. *Freshwater Science* 35(2): 559–572. © 2016 by The Society for Freshwater Science.
- II Mustonen K-R, Mykrä H, Marttila H, Sarremejane R, Veijalainen N, Sippel K, Muotka T & Hawkins C (2016) Reduced flow seasonality as a key determinant of boreal stream invertebrate communities under climate change. Manuscript.
- III Mustonen K-R, Mykrä H, Louhi P, Markkola A, Tolkkinen M, Huusko A, Alioravainen N, Lehtinen S & Muotka T (2016) Sediments and flow have mainly independent effects on multitrophic stream communities and ecosystem functions. *Ecological Applications* 26(7): 2116–2129. © 2016 by the Ecological Society of America.

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